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THE MEASUREMENT OF DROUGHT RESISTANCE IN WHEAT BY FIELD AND LABORATORY METHODS

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THE MEASUREMENT OF DROUGHT RESISTANCE IN WHEAT BY FIELD AND LABORATORY METHODS

H. B. Peto

I. INTRODUCTION

The economic importance of resistance to drought has furnished the main incentive for scientific investigation of the problem. In the semi-arid regions of the United States and Canada, where moisture is generally the most important factor limiting plant growth, plant breeders are giving a great deal of attention to the development of drought resistant wheat varieties. However, little progress has yet been made in this direction.

In Russia, the breeding of drought resistant wheats has been in progress for a longer period of time, and several new wheat varieties, superior also in yield and quality to the old Russian varieties have been produced.

In 1929 a breeding investigation of drought resistance was commenced at the University of Alberta, Edmonton. New varieties were introduced from Russia and crossed with local varieties. The F_8 hybrids obtained from these crosses have been used in the present investigation which was begun in October 1935, and has been

continued up to the time of writing. The aim has been to develop methods of measuring drought resistance in wheat, which will aid in the selection of new varieties capable of yielding a satisfactory crop under conditions of limited moisture supply.

This investigation follows three lines of procedure:

1. The carrying on of field tests as a means of selecting varieties with regard to their yield under drought conditions.
2. The development of laboratory methods which will differentiate varieties highly drought resistant from those non-drought resistant, and thus improve the general level of the material subjected to field tests.
3. The study of characters which may be later shown to be genetically associated with drought resistance, such as, number of stomata per unit area of leaf surface, number of tillers per plant and height.

In the following pages the experiments are grouped according to the particular aspect of the subject to which they pertain.

II. REVIEW OF LITERATURE

From a review of the literature on the physiology of drought resistance it seems that certain morphological and physiological changes run hand in hand when plants are exposed to drought. Maximov (8) believes that morphological changes are associated, for the most part, with physiological changes which are brought about in response to drought, and that these physiological characters are the basis of drought endurance. Briefly, Maximov believes that true resistance lies in the inherent ability of the plant cells to withstand drought without much injury.

A review of a few experiments which might bear out Maximov's hypothesis would not be out of place. According to Maximov (8), Tumanov carried out a wilting experiment with eight varieties of wheat which he believed varied in their drought resistance. The results indicated that the resistant varieties had a survival percentage of not less than 80, whereas the susceptible varieties had a survival percentage of about 50.

The problem of drought resistance is greatly aggravated by the presence of two kinds of drought: soil drought and atmospheric drought. Tumanov (18), working with cereals, soybeans, alfalfa and sorghums, studied

the effects of soil drought when watering was stopped at the shooting stage in cereals, and at the flowering stage in the dicotyledons. The degree of drought resistance was measured by the number of dead leaves after eight days with no available water. The percentage survival of leaves varied from 0 in oats to 84 in alfalfa. The percentage of dead leaves was not always found to be a good criterion of drought resistance as the resistance varied considerably in the different plant organs. For example, a lower drought resistance was found in the aerial parts of alfalfa than in the root-crown and roots.

Kondo (6), working with soybeans and sunflowers, also studied the effects of soil drought and showed that plants subjected to wilting in the later stages of development suffered more from loss of leaves than plants in the early stages. The greater the loss of leaves, the greater the depression of yield. It was found that the stage of development of the plant played an important part in the resistance to dehydration.

The effect of atmospheric drought has been studied under controlled conditions by T. A. Krasnoselsky -Maximov (7). The plants were exposed to an artifical dry wind at 18 - 26 % relative humidity, a temperature of 40 - 45° C, a soil moisture of 60 % of its water holding capacity, and

a wind velocity of 3 metres per second. The usual time for the experiment was eight hours. It was found that wheat plants suffered from dry wind differently at different stages of growth. The injury was greatest at the time of earing and flowering, less at the stage of milky ripeness and least of all at waxy ripeness. The absolute dry weight of the grain increased as exposure to the dry wind was delayed. When the leaves were removed more water entered the inflorescence, thus giving a higher grain weight. Kondo, on the other hand, found that a lower seed yield and total yield of soybeans and sunflowers corresponded to the loss in leaf surface.

Maximov found that the greater the soil drought at the time of exposure to the dry wind, the greater was the injury. At a soil moisture of 20 % of its water holding capacity the lower leaves were killed by soil drought and the upper leaves and inflorescence by the dry wind. While at 40 % of the moisture holding capacity death of the lower leaves occurred, thus putting them out of competition for water and consquently the inflorescence and upper leaves went without injury for some time. At 60 % moisture, the lower leaves took all the moisture from the soil, thus resulting in injury to the upper leaves and inflorescence.

With reference to Maximov's statement that "the only true criterion of drought resistance is the ability of the plant to resist severe dehydration of its cells

without injury", the question arises as to what might be the inherent properties of resistant plants that allow them to withstand desiccation of their cells without injury.

Newton and Martin (10) have made physico-chemical studies of drought resistance in a number of crop plants. The two principle methods were to determine the osmotic pressure and the bound water content of the tissue fluids. The osmotic pressure of the tissue fluids was found to vary with the physiological scarcity of water, but was not considered a reliable index of drought resistance. Bound water content gave satisfactory results, as it was possible to arrange a number of cultivated wheats and grasses in order of their drought resistance. These authors suggest that it is the high colloidal content of plant cells, which reduces the abstraction of water from them. They also hypothesize that this may account for the lack of injury shown in some plants and not in others under severe drought conditions.

Vasilev (19) concludes that the accumulation of soluble carbohydrates by the plant, under conditions of insufficient water supply, is a means of increasing its drought resistance. The expenditure of reserve carbohydrates, with permanent wilting, is one of the immediate

causes of desiccation. He also suggests that the protective action of sugars against desiccation is analogous to their protective role in plants exposed to frost.

III. LABORATORY EXPERIMENTS WITH THE DROUGHT MACHINE

REVIEW OF LITERATURE

One of the first methods of measuring drought resistance by artificial means was developed in Russia by Dr. T. A. Krasnoselsky-Maximov of the Institute of Plant Industry in Leningrad (1, 7). He constructed a glassed-in cabinet with a rotating table to test plants for resistance to "windburn". The table had a capacity of six pots. The wind velocity was approximately three metres per second, with a temperature of 37 - 39° C. and a relative humidity of about 16 - 18 %.

Shirley (13,14) has described an apparatus the construction of which is somewhat like that of Maximov's for testing the drought resistance of conifers.

Hunter, Laude and Brunson (5) made a simple heat chamber with thermostatically controlled heating units. A constant motion of air and uniformity of temperature were maintained by means of a small electric fan. Tests were made with 14 - day old corn seedlings. They were placed in the heat chamber and exposed to a temperature of 114° F. for 6½ hours. Essentially the same order of relative

resistance was obtained with seedlings as was noted for the plants in the field.

Bayles and co-workers (2) by means of a heating unit, fan and revolving table were able to produce artificial drought conditions in the greenhouse. Eight varieties of wheat at the shooting stage were exposed to a current of air at a temperature of 92° to 98° F. for 24 hours. Differences in the amount of injury between the varieties Baart and Hope, for example, were clearly demonstrated, but smaller differences between other varieties were not so clearly brought out.

In 1932 a drought machine (Fig. I) was constructed at the University of Alberta, Edmonton, under the direction of Dr. O. S. Aamodt. This machine was patterned after the one built by Maximov.

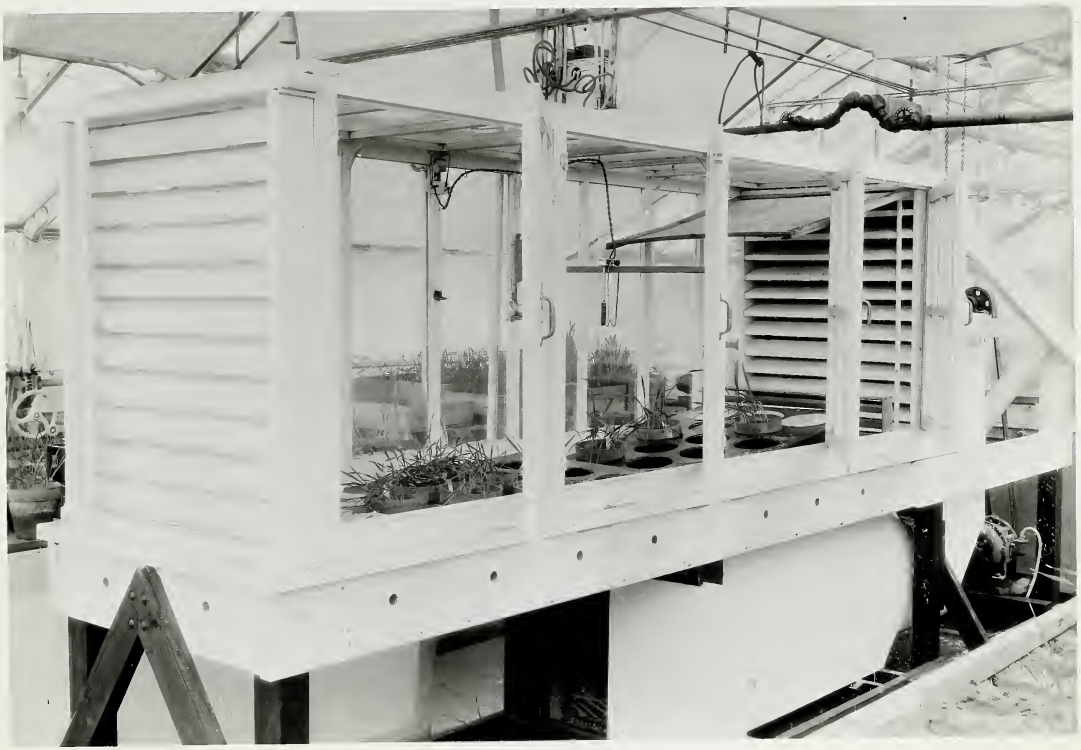

Fig. I. Front view of the drought machine showing the glass tunnel with baffle plates in front of the fan and at the end of the tunnel. The air intake and the chamber containing electric heating coils are shown underneath the glass tunnel. The floor of the tunnel shows the pots submerged below the path of the hot winds. The pots are placed in moist sand.

DEVELOPMENT OF METHODS AND CONSTRUCTION OF EQUIPMENT

When the present investigation was begun in the fall of 1935 some alternations in the drought machine were found to be necessary before satisfactory results could be expected.

The velocity of the wind in the cabinet varied from six to twelve miles per hour. Thus, a uniform treatment could not be assured for all varieties, even though the pots were periodically moved from one location to another in the cabinet. There was also difficulty in maintaining a constant air temperature in the machine. As air was drawn in from the room, the temperature in the cabinet was readily affected by the room temperature. Several hours were needed to heat the greenhouse before an experiment could be started.

A considerable amount of time was spent at the outset of this investigation remodelling the drought machine to overcome the above mentioned difficulties. A picture of the remodelled machine is shown in Fig. II.

The following improvements have been made. First, uniform conditions for all plants have been secured by means of an endless chain to which 25 pots are fastened. The endless chain is kept in constant motion and all the pots

Fig. II. Rear view of the remodelled drought machine showing the endless-belt arrangement to keep the pots in continuous motion, and showing also the return air duct.

make one complete revolution in six minutes. Second, a return air flow has been constructed which makes it possible to keep the greenhouse at ordinary temperatures during the course of an experiment. The temperature can now be raised to the desired level in six or seven minutes, which mater-

ially reduces the cost of operation. Third, a method of watering was devised, whereby the pots were watered from below by means of shallow trays. This method proved to be very satisfactory, as a more uniform distribution of moisture was obtained in all the pots at the time of watering. The porosity of the pots varied considerably and as a result evaporation is greater from the surface of some pots than from that of others. To overcome this the pots were painted on the outside with asphaltum.

EXPERIMENT I.

Methods

The first experiment made in the drought machine was, primarily, a test of methods; the purpose of which was to determine the optimum duration of treatment necessary for the greatest varietal differentiation. Three treatments were used, each one included the same twenty-five varieties* replicated six times. The material consisted of eight varieties from Russia, ten standard local varieties and seven hybrids (three F_6 Caesium x Marquis, two F_7 I-28-60 x Milturum .0321, one F_6 Reward x Caesium and one F_6 Marquis x Caesium).

Five seeds were planted in each pot, and the number of seedlings was reduced to three shortly after emergence.

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* The term "varieties" includes all hybrids and varieties used in the following experiments.

The seeds were germinated in a controlled temperature chamber. A constant temperature of 9° C. was maintained until the seedlings were all showing above the soil. Then the temperature of the chamber was slowly increased for two days to 20° C. On the third day the pots were transferred to outside benches for the remainder of the growing period.

Screened-in cabinets (Fig. III.) were built on the benches to protect the plants from winds and heavy rains. Cotton covers were made for these cabinets (Fig. IV.) in order to shade the plants in very hot weather.

The treatments in the drought machine were delayed a few days longer than was intended owing to harvesting operations at Brooks. Many of the plants were at the heading stage when treated.

The temperature varied not more than a degree above or below 110° F. throughout the treatment in the drought machine. The relative humidity varied from 17 - 23 %, always decreasing with length of run, and all the plants were exposed to the same wind velocity (approximately 6 miles per hour) as a result of the endless chain. The soil temperature increased slowly as the test proceeded, but never reached the temperature of the atmosphere. The highest reading recorded for soil temperature was at the

Fig. III. Screened-in cabinets built to protect the plants from wind and rain.

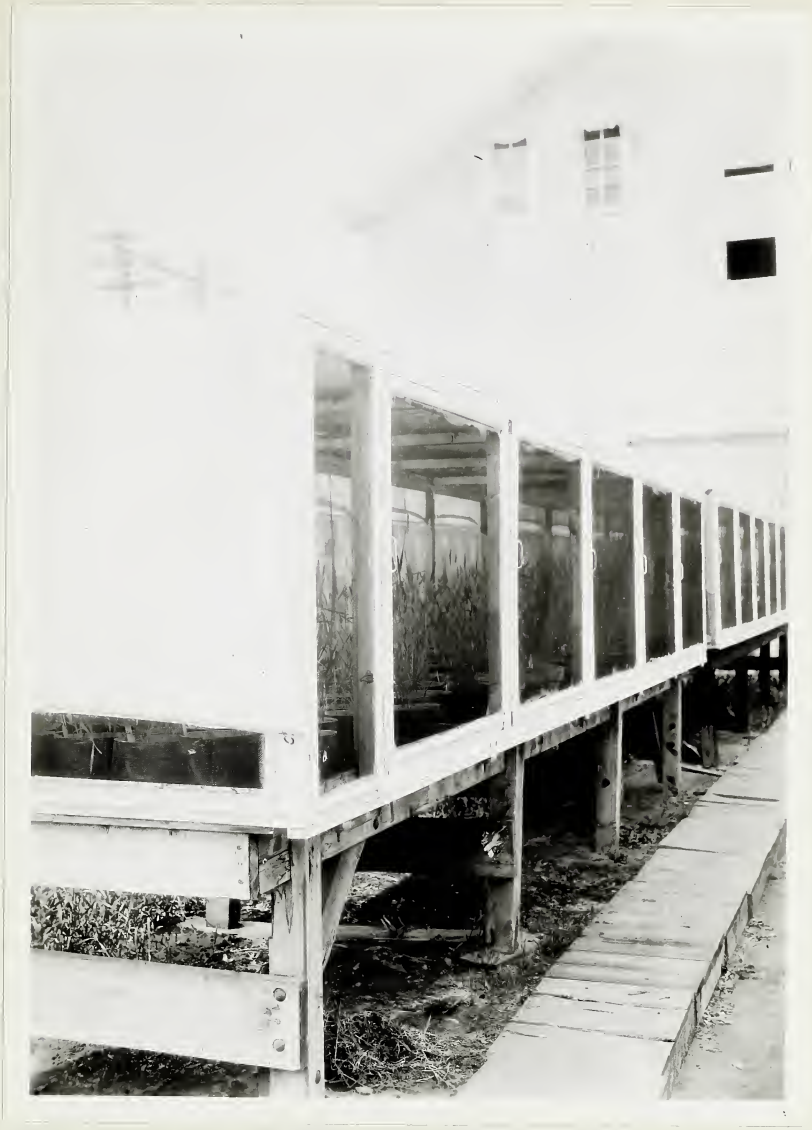


Fig. IV. Cotton covers placed on cabinets to protect the plants in very hot weather.

end of an 18-hour run when it reached 100° F.

The plants were watered in the trays just before going into the drought machine and again immediately after removal.

A survival reading was taken on each run exactly two weeks from the time it was removed from the machine. The basis of calculation of the survival index was as follows:

0 = completely killed. 1 = culm almost killed, practically all leaves damaged.
2 = stem and leaves considerably damaged. 3 = slight damage to leaves and stem.
4 = no damage.

The readings were taken on each individual plant in the pot and an average percentage survival per pot was calculated as follows:

Survival values of the 3 plants per pot.		Average percentage value per pot.
000 =		0 % (completely killed)
111 =	$\frac{25+25+25}{3}$	= 25 %
222 =	$\frac{50+50+50}{3}$	= 50 %
333 =	$\frac{75+75+75}{3}$	= 75 %
444 =	$\frac{100+100+100}{3}$	= 100 % (undamaged)
100 =	$\frac{25+0+0}{3}$	= 8%
110 =	$\frac{25+25+0}{3}$	= 17 %
etc.		etc.

RESULTS

In Table I the varieties are listed in order of general mean survival. The table also includes the mean survival percentage of the varieties in each run (6-hour, 12-hour and 18-hour).

TABLE I

Mean survival indices of wheat varieties in the 6-hour, 12-hour and 18-hour runs of Experiment I.

Variety	N.S.N.*	Survival index			
		6 hr. Mean	12 hr. Mean	18 hr. Mean	General Mean
Garnet	I-25- 13	66.7%	19.5%	9.7%	31.9%
Milturum .0321	I-28- 14	54.2	13.8	8.3	25.4
Reward x Caesium	H-29- 25	40.3	19.5	8.3	22.7
Reward 22-42	I-31- 20	37.7	16.5	11.2	21.8
Caesium .0111	I-28- 20	29.2	11.2	9.7	16.7
Marquis x Caesium	H-29- 48	36.2	9.8	4.2	16.7
Renfrew	I- 0- 20	30.7	15.3	4.2	16.7
Caesium x Marquis	H-29- 57	29.2	15.3	4.2	16.2
Red Bobs 222	I- 0- 18	26.3	16.5	4.2	15.6
Caesium x Marquis	H-29- 71	25.0	11.0	7.2	14.4
I-28-60 x Milt.0321	H-29- 46	26.5	6.8	9.8	14.4
Erythrospermum.0341	I-36-129	26.3	8.3	6.8	13.8
Canus	S-34- 1	29.2	5.5	6.8	13.8
Hard Federation	I-28- 35	29.2	9.2	2.8	13.7
Marquis	I- 0- 9	26.3	4.2	8.3	12.9
I-28-60 x Milt.0321	H-29- 31	29.2	5.5	4.2	12.9
Mindum	I-36-100	27.8	1.3	7.0	12.1
Caesium x Marquis	H-29- 73	25.3	4.8	5.5	11.8
Speltiforme	I-36-122	20.8	5.5	7.0	11.1
Reliance	I-29- 4	32.0	1.3	0.0	11.1
Iumillo No.7	I-36-104	16.7	2.8	7.0	8.8
Hordeiforme .0189	I-36-132	11.2	2.8	1.3	5.1

* University of Alberta Nursery Stock Number.

An analysis of variance was calculated from the data obtained and is presented in Table II. Also an individual

analysis of each run was made and the results are presented in Tables III, IV, and V.

TABLE II

Analysis of variance of the survival indices of the plants treated in the drought machine in Experiment I.

	Degrees of Freedom	Sums of Squares	Mean Square	F.	1%
Varieties	21	12,731.4	6,062.6	39	1.9
Replicates	5	5,671.4	1,134.3		
Runs	2	46,699.8	23,349.9		
Error	367	57,021.6	155.4		
Total	395	122,124.2			

S. E. of a single pot = 12.5

S. E. of variety mean = 2.9

S. E. of difference of any two varieties = 4.1

Significant difference = 8.2

TABLE III

Analysis of variance of the survival indices of the 6-hour run in the drought machine in Experiment I.

	Degrees of Freedom	Sums of Squares	Mean Square	F.	1%
Varieties	21	17,117.0	815.1	7.4	2.0
Replicates	5	9,240.0	1,848.0		
Error	105	20,568.5	110.0		
Total	131	46,925.5			

S. E. of single pot = 10.5

S. E. of variety mean = 4.3

S. E. of difference of any two varieties = 6.1

Significant difference = 12.2

TABLE IV

Analysis of variance of the survival indices of the 12-hour run in the drought machine in Experiment I.

	Degrees of Freedom	Sums of Squares	Mean Square	F.	1%
Varieties	21	4,326.8	206.0	2.4	2.0
Replicates	5	3,330.6	666.1		
Error	105	9,079.9	86.5		
Total	131	16,737.3			

S. E. of a single pot = 9.3

S. E. of variety mean = 3.8

S. E. of difference of any two varieties = 5.4

Significant difference = 10.8

TABLE V

Analysis of variance of the survival indices of the 18-hour run in the drought machine in Experiment I.

	Degrees of Freedom	Sums of Squares	Mean Square	F.	1%
Varieties	21	1,042.6	49.7	1.0	2.0
Replicates	5	5,609.9	1,122.0		
Error	105	5,108.8	49.4		
Total	131	11,761.3			

S. E. of a single pot = 7.0

S. E. of variety mean = 2.9

S. E. of difference of any two varieties = 4.1

The results of the first experiment, summarized in Table I, show a low survival value for all the varieties tested. Little can be said here concerning the relative order of the varieties with respect to drought resistance. The important

point to note is that the statistical analysis of the results (Table II) reveals highly significant differences between the general means of varieties. In the individual analysis for the 6, 12 and 18 hour runs, (Tables III, IV and V) the variance due to varieties significantly exceeds that due to error in the 6 and 12-hour runs only, the excess being greater in the 6 hour run. The necessary significant differences are 12.2 and 10.8 for the 6 and 12-hour runs respectively. The replicate differences were highly significant for all runs. The reason for these differences are discussed under the next heading.

DISCUSSION OF THE DIURNAL EFFECT

Very marked differences in the survival values were noticed between replicate tests, and it seemed quite evident that these differences varied according to the time of day at which the plants were treated in the drought machine. For example, the total survival of all varieties for each six-hour run when plotted showed that considerable injury occurred during the test made in the morning hours from 5 a.m. to 11 a.m., and less injury in the afternoon, evening and night tests. (Fig. V). The four periods of the day were designated A. (5 a.m. to 11 a.m.), B. (11 a.m. to 5 p.m.), C. (5 p.m. to 11 p.m.) and D. (11 p.m. to 5 a.m.).

In the 12-hour run a more pronounced contrast was shown between the day and night tests. The injury during the D A period was definitely greater than that during the B C period.

In the 18-hour run the injury was greatest when the number of hours of daylight exceeded the number of hours of darkness.

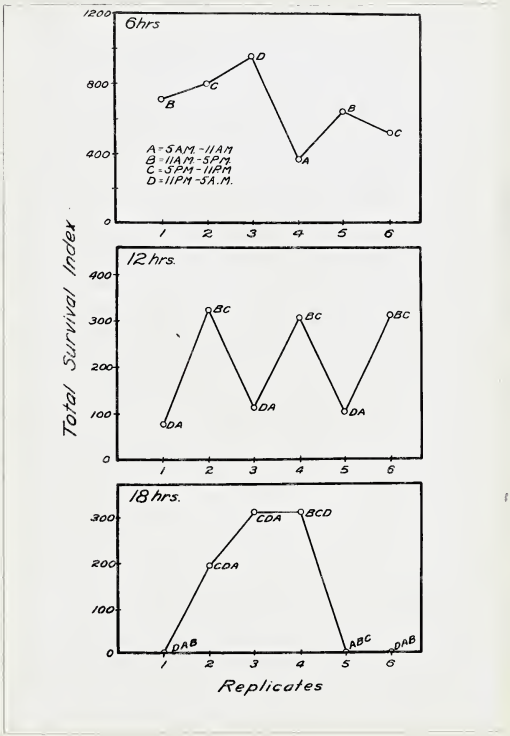


Fig. V. Showing the diurnal effect in the 6, 12 and 18-hour drought machine runs. Each point represents the total survival for one replicate.

RELATIONSHIPS BETWEEN RUNS

The relationships between survivals in the 6, 12 and 18-hour runs were determined by means of the correlation coefficient. The results are summarized in Table VI. The relatively low coefficients for the 12 and 18, and 6 and 18-hour runs are probably the result of severity of the injury sustained in the 18 hour run.

TABLE VI

Coefficients of correlation between survival values of the 6-hour, 12-hour, and 18-hour runs in the drought machine in Experiment I.

Variables correlated	No. of Varieties.	Correlation coefficient
6-hour and 12-hour	22	.64*
12-hour and 18-hour	22	.36
6-hour and 18-hour	22	.38

* Exceeds 1% point.

SUMMARY

It is apparent from the above results that the varieties did not all respond alike to treatment in the drought ma chine and, further, the injury is more severe

when tests are made during the day than during the night. The morning period (5 a.m. to 11 a.m.) is more damaging than is the afternoon period.

EXPERIMENT II.

Methods

A number of Russian varieties were included in this experiment on the recommendations of Dr. G. K. Meister of Saratov, U. S. S. R., who visited the laboratory at the University of Alberta during the summer of 1936. The varieties he suggested, not included in the last experiment, were Lutescens .062, Erythrospermum .0841, Graecum .0283, Albidum .0604 and Melanopus .069. The 25 varieties in this run consisted of 10 varieties from Russia, 9 standard local varieties and 6 hybrids.

With the help of Dr. C. H. Goulden of the Dominion Rust Laboratory, Winnipeg, the experiment was planned in such a manner as to take into account the diurnal variation in the analysis of variance. The day was divided into four 6-hour periods represented by the letters A B C D, and four different combinations of runs were made up for each treatment as represented in Diagram 1.

Diagram 1.

Type and frequency of runs made in the drought machine in Experiment II.

Type	Frequency	Possible Combinations	
18 X	1	A B C	18-hour runs:- 3 contain A and 1 does not.
" Y	3	B C D	
" X	1	C D A	
" X	1	D A B	
12 X	1	A B	12-hour runs:- 2 contain A and 2 do not.
" Y	2	B C	
" Y	1	C D	
" X	2	D A	
6 X	3	A	6-hour runs:- 1 contains A and 3 do not.
" Y	1	B	
" Y	1	C	
" Y	1	D	

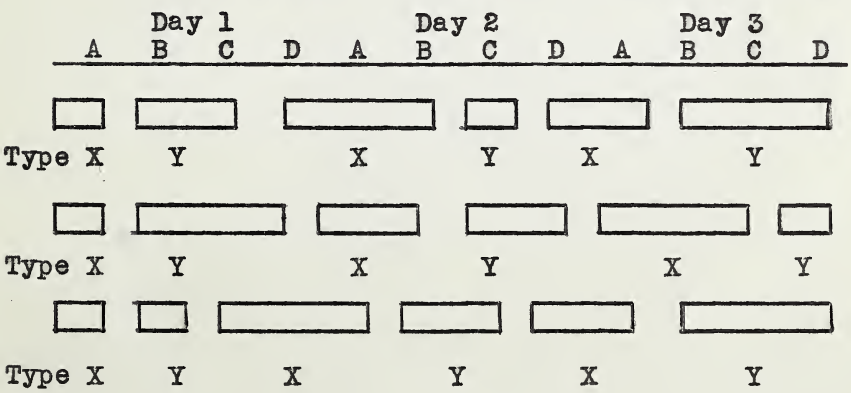
Three of the 18-hour runs contained A which is the morning period and one did not. For the 12-hour runs two contained A and two did not; and for the 6-hour runs one contained A and three did not. These were regarded as two

general types X and Y, the former representing runs that contained A and the latter runs that did not.

The runs were arranged in the order given (Diagram 2), in which the 9 days required to complete the 6 replications were divided into three groups of 3; each 3-day period gave 2 complete replications. The X's and Y's were alternated, there being an equal number of X and Y types of each length of run. This was indicated in Diagram 1 under the heading "Frequency". Consequently, in disregarding the difference, say, between the 12-hour runs B C and C D a direct comparison could be made between X and Y types.

Diagram 2.

The length and order of runs in the drought machine (shown diagramatically by a double line). A = 6 a.m. - 12 noon, B = 12 noon - 6 p.m., C = 6 p.m. - 12 mt., D = 12 mt. - 6 a.m.



The same conditions were maintained in the second experiment as in the first, the machine was operated continuously in order that all the material would be tested at as nearly the same stage of development as possible. This time, however, the plants were watered 6 hours before being transferred to the drought machine, and again 12 hours after removal from it.

RESULTS

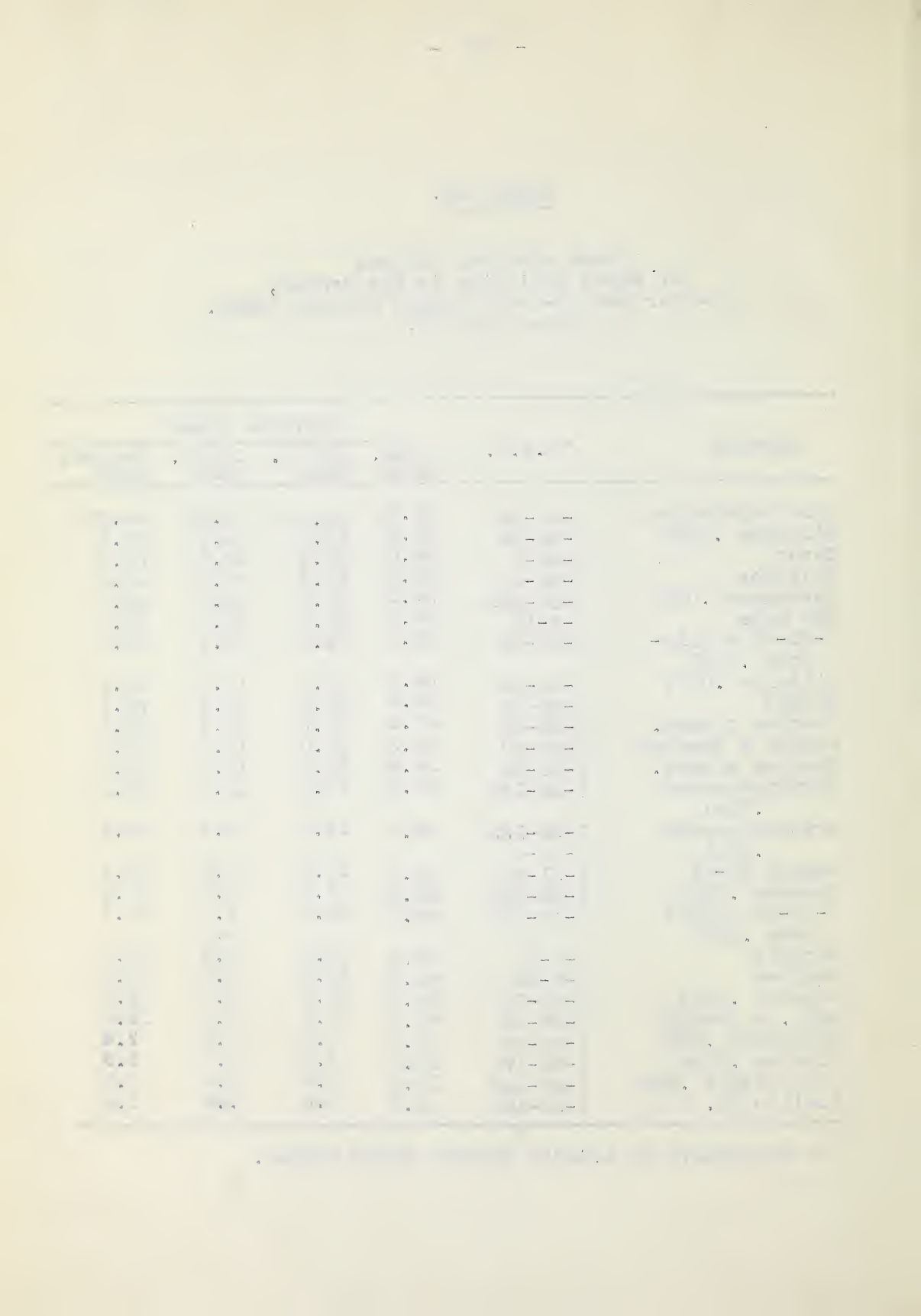
Mean survival indices for the different varieties in the 6, 12 and 18-hour runs together with a general mean for each variety are recorded in Table VII. The varieties are ranked according to the general mean survival.

TABLE VII.

Mean survival indices
of wheat varieties in the 6-hour,
12-hour and 18-hour drought machine tests
in Experiment II.

Variety	*N.S.N.	Survival Index			
		6 hr. Mean	12 hr. Mean	18 hr. Mean	General Mean
Hard Federation	I-28-35	79.2%	30.5%	24.8%	44.9%
Milturum .0321	I-28-14	69.3	43.0	15.3	42.6
Canus	S-34-1	64.0	37.3	16.7	39.3
Reliance	I-29-4	69.3	27.8	20.8	39.3
Lutescens .062	I-36-128	58.3	29.2	16.7	34.7
Red Bobs	I-o-18	59.7	27.7	13.7	33.7
I-28-60 x Milturum .0321	H-29-46	52.8	23.5	20.8	32.4
Milturum .0274	I-28-25	54.0	20.8	18.0	30.9
Garnet	I-25-13	54.2	23.5	15.2	30.9
Caesium x Marq.	H-29-57	47.3	29.3	15.2	30.6
Reward x Caesium	H-29-27	58.3	14.0	14.0	28.8
Caesium x Marq.	H-29-54	38.8	26.3	16.7	27.3
Erythrospermum .0341	I-36-129	44.3	17.8	13.8	25.3
Erythrospermum .0841	I-36-133	38.8	13.8	18.2	23.6
Reward 22-42	I-31-20	41.7	18.2	11.0	23.6
Graecum .0283	I-36-130	45.0	17.7	8.5	23.1
I-28-60 x Milturum .0321	H-29-31	40.2	15.3	9.7	21.7
Marquis	I-0-9	50.0	6.8	8.3	21.7
Renfrew	I-0-20	43.2	13.8	5.5	20.8
Caesium .0111	I-28-20	39.0	12.5	5.5	19.0
Marq. x Caesium	H-29-48	44.5	4.2	8.3	19.0
Melanopus .069	I-28-15	16.7	4.2	1.3	7.4
Albidum .0604	I-28-19	18.0	2.8	0.0	6.9
Hordeiforme .0189	I-36-132	15.3	2.8	0.0	6.1
Iumillo No. 7	I-36-104	4.2	1.3	000	1.8

* University of Alberta Nursery Stock Number.



Comparing the mean survival values of Table VII and Table I, Milturum .0321 was second highest in both cases, Red Bobs 222 and I-28-60 x Milturum .0321 (H-29-46) occupied an intermediate position, while Hordeiforme .0189 and Iumillo were consistently low in both experiments. This does not necessarily mean that Milturum .0321 is definitely more drought resistant than Hordeiforme .0189 and Iumillo, but these experiments do show that varieties react differently to treatment in the drought machine. This point will be discussed more fully later, in relation to the correlations made between the runs of these experiments.

A complete analysis was calculated from the data obtained and is presented in Table VIII. Individual analysis for each length of run is presented in Tables IX, X and XI.

TABLE VIII.

Analysis of variance
of the survival indices for the
drought machine tests in Experiment II.
(Table VII)

	Degrees of Freedom	Sums of Squares	Mean Square	F	5%	1%
Varieties	24	55,876.0	2,328.1	6.9*		2.2
Replicates	12	30,966.9	2,580.6			
X Y	1	28,021.3	28,021.3			
Runs	2	96,467.1	48,233.5			
X Y x Runs	2	11,245.6	5,622.8			
Varieties x X Y	24	6,998.1	291.6	1.29**	1.55	
" x Runs	48	16,111.4	335.6	1.49**	1.32	
Var. x Runs x X Y	48	7,868.3	163.9			
Residual	288	64,841.1	225.2			
Total	449	318,395.8				

S.E. of a single pot = 18.3

S.E. of variety mean = 4.3

S.E. of difference of any two varieties = 6.1

Significant difference = 12.2

* Varieties x Runs was employed in obtaining the F value of varieties.

** Residual error was employed in obtaining the F value of interactions.

TABLE IX

Analysis of variance of the survival indices for the 6-hour treatment in the drought machine experiment II.

	Degrees of Freedom	Sums of Squares	Mean Square	F.	1%
Varieties	24	46,555.3	1,939.8	6.6	2.0
Replicates	4	13,696.8	3,424.2	11.7	3.5
X Y	1	33,182.1	33,182.1	113.5	6.9
X Y x Varieties	24	7,459.1	310.8		
Residual	96	28,057.6	292.3		
Total	142	128,950.9			

S. E. of single pot = 17.1

S. E. of variety mean = 7.0

S. E. of difference of any two varieties = 9.9

Significant difference = 19.8

TABLE X

Analysis of variance of the survival indices for the 12-hour treatment in the drought machine in Experiment II.

	Degrees of Freedom	Sums of Squares	Mean Square	F.	1%
Varieties	24	18,369.3	765.4	3.8	2.0
Replicates	4	15,366.1	3,841.5	19.0	3.5
X Y	1	4,309.4	4,309.4	21.4	6.9
X Y x Varieties	24	4,871.2	203.0		
Residual	96	19,374.3	201.8		
Total	149	62,290.3			

S. E. of a single pot = 14.2

S. E. of variety mean = 5.8

S. E. of difference of any two varieties = 8.2

Significant difference = 16.4

TABLE XI

Analysis of variance of the survival indices for the 18-hour treatment in the drought machine in Experiment II.

	Degrees of Freedom	Sums of Squares	Mean Square	F.	5%	1%
Varieties	24	7,062.7	294.3	1.6	1.6	
Replicates	4	1,934.4	483.6	2.7	2.5	
X Y	1	1,775.1	1,775.0	9.8		6.9
X Y x Varieties	24	2,536.0	105.7			
Residual	96	17,378.9	181.0			
Total	149	30,687.1				

S. E. of a single pot = 13.5

S. E. of variety mean = 5.5

S. E. of difference of any two varieties = 7.8

Significant difference = 15.6

Statistical analysis of the results (Table VIII) reveals highly significant differences between the general means of varieties. A difference of ~~10~~ 12.2 units between means corresponds approximately to the 5% point. The interaction of the varieties and runs was employed as a measure of the error of varietal comparisons. The variance for X Y which measures the difference between runs containing morning periods and those that do not, is, as expected, quite significant. The interaction X Y x runs, also is significant.

Considering the individual analysis for each length of run (Tables IX, X and XI), the F value for varieties was the largest for the 6-hour run. This indicates that this particular length of run is the most efficient for classifying varieties on the basis of response to artificial drought.

DISCUSSION OF THE DIURNAL EFFECT

The effect of time of day on survival is graphically represented in Fig. VI. Three replicates of each run contained the A period (X) and three did not (Y). In Fig. VI each point represents the total survival of one replicate. The depressing effect of the A period on survival is quite apparent in the upper section of the figure representing the 6-hour runs.

The drop of the curve in the D period for the 6-hour run, however cannot be explained. The C D period in the 12-hour run showed a low survival index, but it is doubtful whether any significance can be attached to this value at present, as no runs were made during the same period in the first experiment with which to compare it.

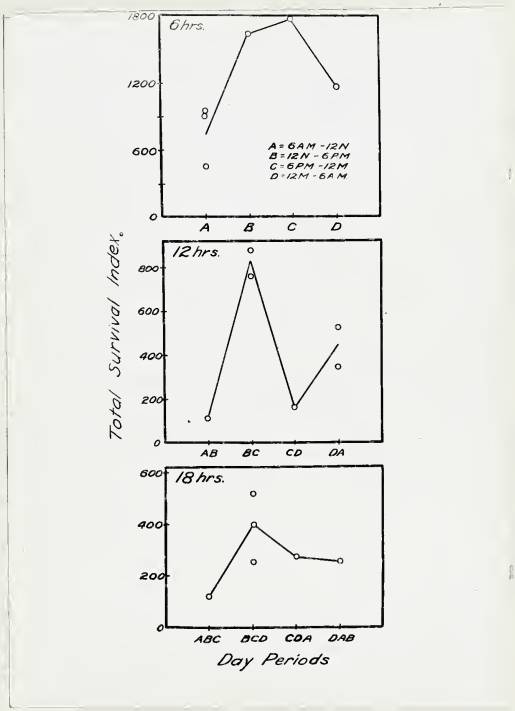


Fig. VI. Showing the diurnal effect in the 6, 12 and 18-hour drought machine runs. Each point represents the total survival for one replicate.

Apart from the two differences mentioned, the same conclusion can be drawn here as from Experiment I, namely, that there is a definite diurnal effect. The period

of the day that brings about the greatest injury in the drought test is the morning period from 6 a.m. to 12 p.m. Considerably less injury occurs in the afternoon, evening and night periods. In the 12 and 18-hour runs the position of A in the run is important. When A is present at the beginning of a run the plants suffer greater injury than when it is in the middle or at the end.

RELATIONSHIPS BETWEEN RUNS AND BETWEEN EXPERIMENTS

The coefficients of correlation between the three runs of Experiment II are given in Table XII.

TABLE XII

Coefficients of correlation between the survival values of the 6 hour, 12-hour and 18-hour runs of Exp.II.

Variables correlated	No. of Varieties	Correlation Coefficient
6-hour and 12-hour	25	.81*
12 " " 18 "	25	.85*
6 " " 18 "	25	.78*

* Exceeds 1% point.

The coefficients of correlation between the three treatments are statistically significant with a P value in each case exceeding the 1% point. The magnitude of the

coefficients suggests that the interaction between varieties and runs (Table VIII) though significant is relatively unimportant.

The coefficients of correlation between varieties in the first and second experiments are given in Table XIII.

TABLE XIII

Coefficients of correlation between varieties of Experiment I, and Experiment II.

Variables correlated	No. of Varieties.	Correlation Coefficient
6 hours and 6 hours	17	.48*
12 " " 12 "	17	.33
18 " " 18 "	17	.04
Mean " Mean	17	.41

* Exceeds 5% point.

The coefficient is statistically significant only in the case of the 6-hour runs. Such a result would be expected from a consideration of the previous analyses of the individual runs of both experiments.

The lack of correlation found between the 12-hour and between the 18-hour runs of both experiments can be attri-

buted to the severity of these runs. General observations during the runs also bear out this point.

SUMMARY

The results so far secured indicate that varietal differences with respect to treatment in the drought machine are highly significant, and that there is a correlation between the 6-hour runs in the two experiments.

The presence of a diurnal effect has been definitely established; greater damage resulted from tests made during the morning hours from approximately 6 a.m. to 12 noon, than during any other period of the day. To establish the cause of this diurnal variation would in itself necessitate a distinct research project. It is sufficient here to notice this effect, and plan the experiments in such a way as to take this phenomenon into account.

IV. LABORATORY EXPERIMENTS WITH SUGAR SOLUTIONS

REVIEW OF LITERATURE

According to Timofeeva (17), wheat varieties can be classified with respect to drought resistance on the basis of seedling tolerance to sugar solutions. His work is based on two theories:

(1) That drought resistance is conditioned by the capacity of the protoplasm to withstand strong water deficiency (Maximov).

(2) That a cell can withstand plasmolysis without losing its viability (Tumanov).

Timofeeva subjected wheat seedlings to sugar solutions of varying concentrations (from a 1-molar solution to a saturated solution). He found that a greater percentage of drought resistant varieties survived than did those which were non-resistant.

Ohga (11), using a similar method to that of Timofeeva, found that when the young seedlings are placed in a sugar solution of higher molecular concentration than that necessary to plasmolyze the cells, they wilt at first, but recover and continue to live.

It might be interesting to note another artificial method used in measuring drought resistance. Bolsunov (3),

Snoep (16) and Pavlov (12) have studied the effect of germinating seeds in sugar and salt solutions. Bolsunov, working with wheat, has germinated seed in solutions of concentrations of 10 to 15 atmospheres. He found that the plants which showed the highest survival in these solutions gave the greatest yield in the field. Aamodt and his assistants in 1934 (unpublished), at the University of Alberta have shown that some varieties germinate more rapidly than others in different concentrations of sodium chloride, potassium chloride and sucrose.

Skazkin (15), on the other hand, disagrees with this last method. He states that the method of germinating seeds in sugar solutions does not give a true indication of the osmotic pressure of the seed, nor does it give a reliable figure for the variety which is constant over a number of years. The figure, moreover, is not directly correlated either with drought resistance, cold resistance, yield or earliness.

The present study is based on the work of Timofeeva, the aim being merely to test out this artificial method of selecting drought resistant varieties.

DEVELOPMENT OF METHODS AND CONSTRUCTION OF EQUIPMENT

A considerable amount of time was spent at the outset of this phase of the investigation in developing a satisfactory method of testing the young seedlings in sugar solution. It is not necessary to mention all the different methods tested, but rather to point out the main difficulties encountered and the final method adopted. The various details of the investigation are discussed under separate headings as follows:

1. Elimination of molds.
2. Degree of concentration.
3. Stage of development of plant before treatment.
4. Effect of nutrients in the sugar solution.
5. Duration of sugar treatment and outline of standard method adopted.

Elimination of Molds

Probably one of the most important difficulties that had to be overcome was the elimination of molds during the sugar treatment. Sugar being a favorable medium for the growth of fungi made the problem of elimination more difficult. Molds persisted, even though all the solutions and equipment were sterilized and the seed was surface-

sterilized for 2 minutes in mercuric chloride (1-1000).

As the seed used in these experiments was quite wrinkled, it was felt that a longer period of surface-sterilization in mercuric chloride was necessary. A preliminary test was made merely to indicate whether or not the duration of treatment in mercuric chloride could be increased without impairing germination.

Eight duplicate lots of 100 seeds of Reward wheat were counted out and each duplicate lot was exposed to a different period of time in mercuric chloride (1-1000). The seeds were then germinated and counts made. The results of the germination test are presented in Table XIV.

TABLE XIV

The germination percentage of Reward wheat for the different periods of surface-sterilization in mercuric chloride (1-1000).

Period of treatment	Percentage Germination		
	1st lot	2nd lot	Average
3 minutes	85%	87%	86%
5 "	88	85	87
10 "	90	89	90
20 "	90	90	90
30 "	90	95	93
40 "	85	83	84
50 "	79	81	80
60 "	71	73	72

The results indicate that the duration of treatment of seed in mercuric chloride for surface-sterilization can be increased to 20 or 30 minutes without affecting the percentage germination. However beyond 30 minutes there seems to be a slowing up as well as a decrease in germination.

In the experiments that followed, all the seeds were surface-sterilized for 20 minutes. As a result of this treatment all signs of molds were completely eliminated.

Degree of Concentration

Timofeeva (17) claims that concentrations of the sugar solution above 1 molar do not affect the relative behavior of drought resistant and non-drought resistant varieties. Any concentration above the point of "incipient plasmolysis" ensures plasmolysis of all cells and thus water is withheld from the cells of all varieties to the same extent.

A 2-molar solution of sucrose was decided upon as this concentration is sufficient to withhold water from the roots.

Stage of Development of Plants before Treatment

An experiment was carried out in which the wheat

seedlings were exposed to sugar treatment at two stages of development, namely, 6 and 8 days from the time the seeds were placed in the germinator.

Duplicate lots of 25 seeds were counted out for two varieties, Marquis and Milturum .0321. Each lot of seed was surface-sterilized and washed in distilled water. The seeds were germinated between sterile blotters at a temperature of 15 to 17° C. After 6 days in the germinator the roots had reached a length of about one inch, and the coleoptiles ¼ inch. Then one-half of the young seedlings were transferred from the blotters to wire meshed screens, and the roots immersed in a 2-molar sugar solution for 4 days. The other half of the seedlings were allowed to germinate for 10 days before being exposed to the same sugar treatment. The roots in this case were 5 inches and the stems 4 inches long.

After the sugar treatment, the roots were washed in distilled water and the young seedlings planted in pots and grown in the greenhouse at approximately 60° C. Two weeks after planting a survival percentage was taken.

TABLE XV

Percentage survival of wheat plants treated in a 2-molar solution of sucrose for 4 days at two different stages of growth (6 and 10 days after the time seeds were put in germinator).

Number of days allowed to germinate before treatment.	Number of plants survived	Percentage survival based on 25 plants
6 days Marquis	23	92
6 " Milturum .0321	23	92
10 " Marquis	2	8
10 " Milturum .0321	4	16

The results in Table XV indicate that the treatment of the plants germinated for 6 days was not drastic enough and that of those germinated for 10 days probably too drastic. There should be an optimum stage of development for the best varietal differentiation somewhere between these two treatments. Possibly the best time would be from one to two days after the coleoptiles have reached a growth of from $\frac{1}{4}$ to $\frac{1}{2}$ inch in length, and the roots approximately 1 inch in length. A shortage of wire screens prevented the

duplication of tests.

Effect of Nutrients in the Sugar Solution

Dr. A. G. McCalla suggested a factor which had not previously been considered, namely, the starving of plants during treatment.

Two tests were made to see whether or not nutrients showed any effect when present in the sugar solution. Twelve varieties were planted in duplicate. The seed was surface-sterilized for 20 minutes, washed in sterile distilled water and germinated on screens in moist sand. Each screen contained 25 seeds, and the number of seedlings was reduced to 20 shortly before the sugar treatment. When the seedlings were ready for treatment the sand was removed from under the screens and the sugar solution poured into trays containing these screens. Sufficient solution was used to immerse the roots.

One lot of seed was treated in a 2-molar sugar solution to which was added nutrient solution. The nutrients were made up as follows:

5 cc	(1 molar)	KNO_3
5 cc	"	$CA(NO_3)_2 \cdot 4H_2O$
2 cc	"	$MgSO_4 \cdot 7H_2O$
1 cc	"	$KH_2PO_4 \cdot 7H_2O$
1 cc	.5 % iron tartrate	
14 cc	per litre of solution	

One-quarter of this amount (3.5 cc) was added to each litre of sugar solution. In order to allow for the addition of 3.5 cc of nutrient per litre, 5 cc sugar solution were first removed. This replacement takes care of the difference in molarity between the sugar solution and the nutrient solution.

The second lot of seed was treated in sugar solution only. After 8 days of treatment the screens were removed from the sugar solution, washed in sterile distilled water and the young seedlings planted in sterilized sand to which complete nutrient solution was added in the required amounts. After two weeks growth in sand a survival percentage was taken.

The results presented in Table XVI show that the presence of nutrients does have an effect. That is, greater survival of the seedlings was noticed when nutrients were present in the sugar solution.

A second experiment was made in order to check these results. This time more screens were available, so that 25 varieties could be tested in duplicate. These additional data also indicate the effect of nutrients in sugar solution during a treatment. Over 4 times as many plants survived from the sugar solution plus nutrient (13 plants) as from the sugar solution alone (3 plants).

The number of plants that survived in the whole

TABLE XVI.

The effect of the presence of nutrients in the 2-molar solution in an 8 day treatment. (Percentage based on 20 plants).

Variety Number	Variety	*N.S.N.	Percentage survival	
			In 2-molar sugar solution	In 2-molar sugar solution plus nutrients.
36	Mindum	I-36-100	0	70
12	Marquis	I-0-9	13	67
25	Milturum .0321	I-28-14	0	50
18	Marquis x Caesium	H-29-48	0	40
17	Caesium x Marquis	H-29-71	0	40
14	D. C.	I-60-60	0	40
15	Caesium x Marquis	H-29-73	0	15
6	Reward	I-25-21	0	13
43	Garnet	I-25-13	0	10
22	Reward x Caesium	H-29-22	20	0
4	Caesium .0111	I-28-20	0	0
3	I-28-60 x Milt.	H-29-46	0	0

* University of Alberta Nursery Stock Number

experiment was very low. This can be accounted for by the extremely hot weather during the experiment.

In explaining the above phenomenon one would be inclined to conclude that the roots absorb the nutrients from the sugar solution. However, from the work of Timofeeva and from observations made here, it seems improbable that wheat plants are able to absorb nutrients from a 2-molar sugar solution. A more feasible explanation would be that nutrients are leached from the roots when the young seedlings are placed in the highly concentrated sugar solution. This leaching, however, does not occur, or occurs to a lesser degree, when nutrients are already present in the solution.

Duration of Sugar Treatment and Outline of Standard Method Adopted.

As duration of treatment in the sugar solution is the last factor to be considered, it is now possible to outline a standard method of treatment.

Two durations of treatments were tested in this experiment, viz. 4 and 8 days. The same twenty-two varieties were used here, as were included in Experiment II (drought machine).

The seed was carefully surface-sterilized in

mercuric chloride (1-1000) for 20 minutes and washed in sterile distilled water. The sugar solutions and remaining equipment were also sterilized. The seeds were counted out in duplicate lots of 25 and the number of seedlings was thinned to 20 shortly before treatment. They were then germinated on specially constructed screens (4" x 4"), the latter being arranged in trays (Figure VII).

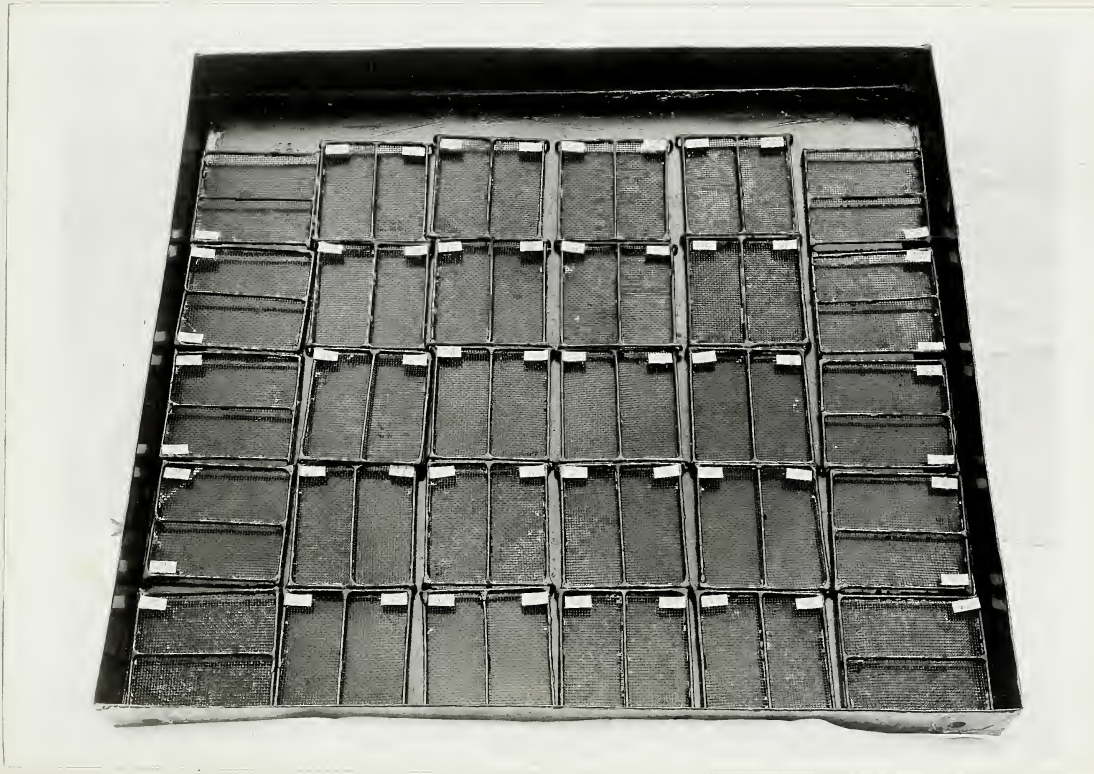


Fig. VII. 4" x 4" screens used in testing the young wheat seedlings in 2-molar sugar solution.

A layer of moist sand was placed in the trays underneath the screens. The trays in turn were covered with moist blotting paper. When the young seedlings had reached a length of about one inch (Fig. VIII), a sufficient amount of a 2-molar solution of sucrose was poured into the trays to submerse the roots.

Fig. VIII. Young wheat seedlings at the stage of growth for treatment in 2-molar sugar solution.

After four (or eight) days had elapsed, the screens were lifted out, washed and then placed in fresh sand and nutrient solution was later added. After 3 weeks the above varieties were classified on the basis of survival. Figure IX shows a screen containing a variety ready for classification.

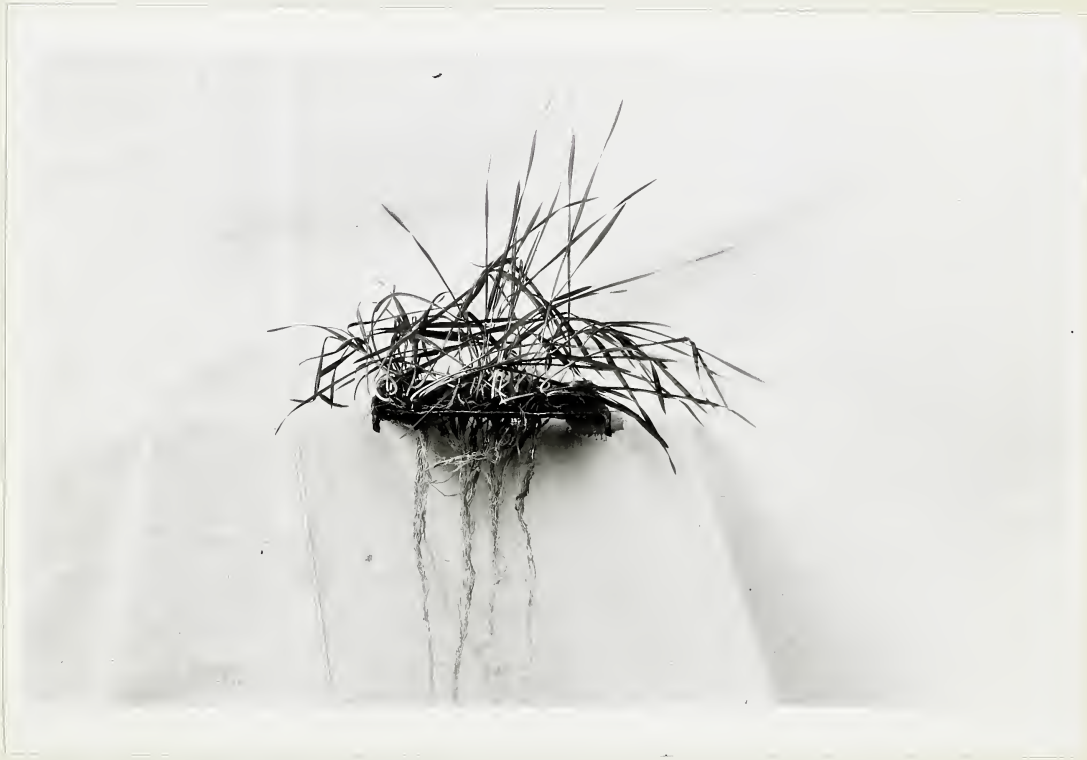


Fig. IX. A screen containing young wheat plants 3 weeks after removal from the 2-molar sugar solution.

The survival readings of the 4- and 8-day treatments are presented in Table XVIII. The varieties are ranked in order of mean survival percentage of the 4-day treatment. The analyses of these data given in Tables XVIX and XX definitely indicate that a varietal difference with regard to tolerance in 2-molar sugar solution exists.

TABLE XVIII.

Survival of plants from the 4-day and 8-day treatments in 2-molar sugar solution (original number of plants being 20 per screen).

Variety	N.S.N.	4-day treatment			8-day treatment		
		Survival Replicates 1.	2.	Mean	Survival Replicates 1.	2.	Mean
Marquis	I-0-9	20	20	20.0	16	11	13.5
Renfrew	I-0-20	20	20	20.0	20	17	18.5
Reward	I-31-20	19	20	19.5	20	20	20.0
Hard Federation	I-28-35	20	19	19.5	11	20	15.5
Erythrospermum .0841	I-36-133	18	20	19.0	10	8	9.0
Red Bobs	I-0-18	18	19	18.5	14	19	16.5
Graecum .0283	I-36-130	20	17	18.5	18	20	19.0
Caesium .0111	I-28-20	20	16	18.0	2	7	4.5
Reward x Caes.	H-29-27	19	17	18.0	20	17	18.5
Hordeiforme .0189	I-36-132	19	16	17.5	7	1	4.0
Caesium x Marq.	H-29-54	19	16	17.5	18	20	19.0
" x "	H-29-57	19	15	17.0	9	11	10.0
Reliance	I-29-4	15	18	16.5	19	17	18.0
Iumillo No. 7	I-36-104	16	16	16.0	18	15	16.5
Milturum .0274	I-28-25	19	13	16.0	17	12	14.5
Canus	S-34-1	15	12	13.5	9	12	10.5
Lutescens .062	I-36-128	15	10	12.5	11	4	7.5
Garnet	I-25-13	16	9	12.5	8	8	8.0
Milturum .0321	I-28-14	14	10	12.0	15	4	9.5
Erythrospermum .0341	I-36-129	12	11	11.5	3	0	1.5
I-28-60 x Milt.	H-29-31	11	11	11.0	12	13	12.5
Caesium x Marq.	H-29-48	9	8	8.5	14	20	17.0

TABLE XIX.

Analysis of variance of the survival of wheat seedlings in the 4-day treatment in a 2-molar sugar solution.

	Degrees of Freedom	Sums of Squares	Mean Square	F	1%
Varieties	21	479.9	22.9	6.7	2.9
Replicates	1	36.4	36.4		
Error	21	71.6	3.4		
Total	43	587.9			

S. E. of single determination = 1.8

S. E. of variety mean = 1.3

S. E. of difference of any two varieties = 1.8

Significant difference = 3.6

TABLE XX

Analysis of variance of the survival of wheat seedlings in the 8-day treatment in a 2-molar sugar solution.

	Degrees of Freedom	Sums of Squares	Mean Square	F.	1%
Varieties	21	1,279.9	61.0	5.4	2.9
Replicates	1	5.1	5.1		
Error	21	239.4	11.4		
Total	43	1,524.4			

S. E. of single determination = 3.4

S. E. of variety mean = 2.4

S. E. of difference of any two varieties = 3.4

Significant difference = 6.8

A slightly higher significance with respect to varietal difference was obtained in the 4-day than in the 8-day period. However, when an additional test was made, using the 4-day treatment, very little injury was noticeable. A further study of this point is necessary before any definite conclusion can be made.

SUMMARY

In summing up the results of this phase of the investigation the important points are as follows:

1. The infection of seeds by molds during a sugar treatment has been completely eliminated by increasing the duration of surface-sterilization of the seed in mercuric chloride (1-1000) to 20 minutes, and by carefully sterilizing all solutions and equipment.
2. The optimum stage of development of seedlings for treatment in the 2-molar sugar solution, is that at which the young stems have reached a length of $\frac{1}{4}$ to $\frac{1}{2}$ inch and the roots approximately one inch.
3. There is a greater survival of seedlings when nutrients are present in the sugar solution than when they are absent.

4. Marked differences between varieties with regard to tolerance of seedlings in sugar solutions have been established; but the most suitable duration of treatment has not been determined.

V. NUMBER OF STOMATA PER UNIT LEAF AREA

REVIEW OF LITERATURE

Miller (9) states that "the number of stomata per unit of leaf surface is, within certain limits, a characteristic of the particular species or variety of plant under consideration."

There seems to be contradictory evidence as to whether environmental conditions influence the number of stomata per unit area of leaf surface. According to Miller (9), Salisbury concludes that the number of stomata per unit surface is mainly dependent on the humidity of the environment, high frequencies being associated with dry exposed conditions, and low frequencies with humid conditions. Miller recorded the number of stomata per unit area of various agricultural plants in the field for several years. Wheat had more stomata on the upper surface of the leaves than on the lower, while the majority of the species had more on the lower than the upper side. The average number of stomata per square inch of leaf surface for wheat was approximately 26,000 on the lower and approximately 37,800 on the upper side.

According to Miller, Eckerson states that there is an inverse relation between the number and size of stomata of

a given type, that is, they are smallest when they occur in the largest numbers. The number of stomata varies on the different leaves of the same plant and on different parts of an individual leaf. Miller (9) cites Yapp, Ray and Salisbury as stating that the upper leaves have more stomata per unit area than the lower. Zalenski established a rule ("Zalenski's Law") as pointed out by Maximov (8) that the anatomical structure of the individual leaves of one and the same shoot is a function of their distance from the root system.

The number of stomata per unit leaf surface varies for different regions of the same leaf. Salisbury found that there was a high frequency at the leaf tip, low frequency at the base and intermediate between the base and apex. He also noted that the number of stomata per unit area increased from the midrib toward the margin. He believes that the increase in frequency of stomata on the various parts of the plant is determined by the water relations. Conditions favoring high rates of transpiration favor high stomatal frequency.

DETERMINATION OF STOMATAL FREQUENCIES

Methods

Stomatal counts were taken per unit leaf area for 81 wheat varieties grown at Edmonton, 75 of which were included in the drought experiment at Brooks. The observations were

made at the time of heading, using on the microscope a low power objective with a No. 10 ocular. The area under magnification was 2.73 sq. mm. Five counts were taken on the upper side of the top leaf of each plant, to one side of the midrib. These counts were made at approximately the same distance from the base of each leaf, this distance being determined by placing the base at the left hand edge of the microscope stage.

RESULTS

The means of each variety in order of decreasing frequency are shown in Table XXI.

TABLE XXI.

Mean frequencies of stomata per unit area of leaf surface for 81 varieties of wheat.

Variety	N.S.N.	Mean of five counts of stomatal frequency per unit area.
Hordeiforme .0189	I-36-132	226
Marquis x Caesium	H-29-48	218
Marquis	I-0-9	216
Caesium x Marquis	H-29-57	212
Ceres	I-25-1	209
Milturum .0321	I-28-14	207
Reward x Caesium	H-29-22	207
Mindum	I-36-100	206
I-28-60 x Milt. .0321	H-29-6	203

(continued)

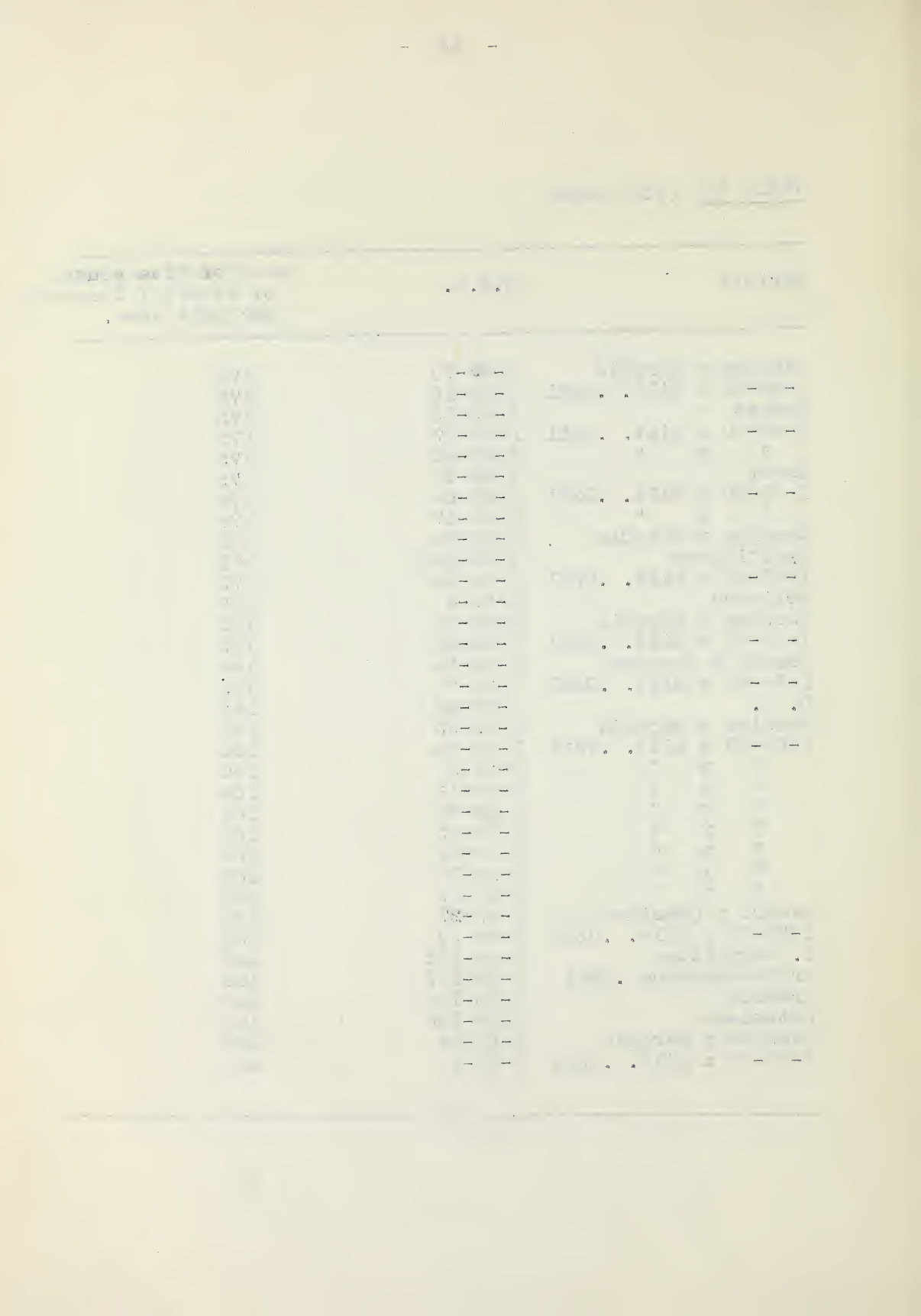
TABLE XXI (continued)

Variety	N.S.N.	Mean of five counts of stomatal frequency per unit area.
Red Bobs 222	I-0-18	203
Caesium x Marquis	H-29-72	200
" x "	H-29-50	199
Canus	S-34-1	197
Milturum .0274	I-28-25	193
I-28-60 x Milt. .0321	H-29-10	191
Caesium x Marquis	H-29-60	190
Renfrew	I-0-20	189
Caesium x Marquis	H-29-54	189
Reward	I-25-21	187
I-28-60 x Milt. .0321	H-29-28	187
" x "	H-29-4	186
Caesium x Marquis	H-29-66	186
I-28-60 x Milt. .0321	H-29-41	186
Caesium x Marquis	H-29-64	186
I-28-60 x Milt. .0321	H-29-30	185
" x "	H-29-46	185
" x "	H-29-32	185
Caesium x Marquis	H-29-52	184
" x "	H-29-71	184
I-28-60 x Milt. .0321	H-29-31	184
Caesium .0111	I-28-20	184
Caesium x Marquis	H-29-62	184
" x "	H-29-58	184
Reward x Caesium	H-29-24	183
Caesium x Marquis	H-29-55	183
I-28-60 x Milt. .0321	H-29-38	182
" x "	H-29-8	182
Reward x Caesium	H-29-23	182
I-28-60 x Milt. .0321	H-29-42	182
Caesium x Marquis	H-29-61	182
Iumillo No. 7	I-36-104	182
Caesium x Marquis	H-29-73	182
" x "	H-29-51	181
Reward x Caesium	H-29-26	180
I-28-60 x Milt. .0321	H-29-37	178
Hard Federation	I-28-35	177
I-28-60 x Milt. .0321	H-29-29	177

(continued)

TABLE XXI (continued)

Variety	N.S.N.	Mean of five counts of stomatal frequency per unit area.
Caesium x Marquis	H-29-70	176
I-28-60 x Milt. .0321	H-29-16	176
Garnet	I-25-13	175
I-28-60 x Milt. .0321	H-29-47	175
" x "	H-29-45	175
Baart	I-33-9	175
I-28-60 x Milt. .0321	H-29-34	174
" x "	H-29-17	174
Caesium x Marquis	H-29-69	171
Speltiforme	I-36-122	171
I-28-60 x Milt. .0321	H-29-43	170
Reliance	I-29-4	167
Caesium x Marquis	H-29-59	166
I-28-60 x Milt. .0321	H-29-40	165
Reward x Caesium	H-29-25	164
I-28-60 x Milt. .0321	H-29-7	163
D. C.	I-28-60	162
Caesium x Marquis	H-29-53	161
I-28-60 x Milt. .0321	H-29-21	160
" x "	H-29-5	160
" x "	H-29-12	159
" x "	H-29-20	159
" x "	H-29-35	158
" x "	H-29-44	156
" x "	H-29-18	151
" x "	H-29-19	150
Reward x Caesium	H-29-27	150
I-28-60 x Milt. .0321	H-29-39	150
T. compactum	I-36-126	145
Erythrospermum .0341	I-36-129	144
Graecum	I-36-124	142
Lutescens	I-36-125	140
Caesium x Marquis	H-29-56	129
I-28-60 x Milt. .0321	H-29-9	114



The mean values show a wide range of frequencies from 114 to 226. That is, the number of stomata per unit area of Hordeiforme .0189 is twice that of I-28-60 x Milturum .0321 (H-29-9).

Statistical analysis of the data by the variance method (Table XXII) reveals highly significant differences between varieties. A difference of 23 stomata between means corresponds approximately to the 5% point. The error involved in the determinations is comparatively small except in the case of certain hybrid strains which were, in all probability segregating.

TABLE XXII

Analysis of variance of stomatal frequency per unit area of leaf surface of 81 varieties of wheat.

	Degrees of Freedom	Sums of Squares	Mean Square	F.	1%
Variety	80	160,176	2,002.2	5.5	1.4
Error	324	118,652	366.2		
Total	404	278,828			

S. E. of single observation = 19.1

S. E. of variety mean = 8.1

S. E. of difference of any two varieties = 11.5

Significant difference = 23.0

In order to see whether the counts varied in the later stages of development of the wheat plant, readings were taken from the same Caesium plot, at late boot, heading and 5 days after heading. Ten readings were taken at each stage of development and are given as follows:

		Mean
Late boot	159-143-187-176-143-156-157-179-189-170	= 167
Heading	199-158-175-141-164-170-161-172-160-142	= 164
Five days after heading	163-142-179-146-172-184-158-183-187-169	= 168

These data would seem to show that the stomatal number per unit area does not vary from the late boot stage until after heading.

Stomatal counts were made in the laboratory in the winter of 1935-36, on a number of the 75 varieties that had been tested in the field. The purpose was to see whether there was sufficient correlation to justify laboratory measurements. The same range of stomatal frequencies existed between the varieties tested in the laboratory as for those tested in the field. However, no correlation was found between the mean varietal frequencies for the two methods. The difference in

the environmental conditions between the laboratory and field may be the cause of this lack of correlation. The light conditions in the greenhouse for the months of January and February were very poor and the plants in general were small and weak. Field observations using the same 81 varieties should be repeated in the summer of 1937, before any definite conclusions can be made.

VI. FIELD EXPERIMENTS AT BROOKS AND EDMONTON

RESULTS

The final selection of drought resistant varieties must be based on field trials. These are expensive, time consuming and, at best, only a few hundred strains can be tested at one time. A further difficulty lies in the fact that yield tests conducted under dry conditions are much more subject to experimental error than are similar tests conducted under more humid conditions.

Last year the field test at Brooks, Alberta, was exposed to very severe drought conditions. There was little or no stand on certain parts of the field. As a result great variations were found between the yields of individual plots.

In 1937 the field trial will be made at Castor, Alberta, where less severe drought conditions are prevalent.

Yield, height and protein data were obtained from the 75 varieties grown at Brooks in triple rows replicated 5 times, and tillering, height and stomatal data were obtained from the same strains grown at Edmonton (height and stomatal tests in single rows, and tillering test in double rows).

Mean values of each variety for the above characters, with the exception of stomata (given on P. 62).are presented in Table XXIII. The varieties are arranged in descending order of yield.

TABLE XXIII

Data obtained from the seventy-five varieties of wheat grown at Brooks and Edmonton.

Variety	N.S.N.	Brooks			Edmonton	
		Yield in gms.	Ht. in inches	Protein %	No. of Tillers	Ht. in inches
I-28-60 x Milt.	H-29-37	155.7	28.0	11.7	13.9	42.0
Caes. x Marq.	H-29-66	149.2	32.0	10.3	12.1	-
Baart	I-33-9	148.8	28.5	10.7	17.9	39.5
I-28-60 x Milt.	H-29-6	141.9	27.5	11.4	13.5	38.0
" x "	H-29-47	138.6	29.0	12.2	12.2	42.0
Renfrew	I-0-20	131.6	31.5	11.2	10.7	42.5
Caes. x Marq.	H-29-62	130.7	30.0	11.3	12.8	41.0
Canus	S-34-1	130.3	27.0	12.0	10.8	39.0
Marquis	I-0-9	130.0	27.0	12.5	10.6	38.0
I-28-60 x Milt.	H-29-44	129.1	26.0	13.1	10.3	39.5
" x "	H-29-45	125.9	30.0	11.4	13.6	42.0
Caes. x Marq.	H-29-53	125.8	30.0	11.2	10.2	42.0
" x "	H-29-54	125.8	33.0	10.0	9.9	42.0
Red Bobs	I-0-18	125.6	30.0	11.8	11.6	39.5
Caes. x Marq.	H-29-58	125.3	31.0	10.4	11.4	42.0
I-28-60 x Milt.	H-29-46	125.1	31.0	10.9	11.8	42.0
" x "	H-29-8	125.1	29.5	11.7	9.5	42.0
" x "	H-29-16	124.5	24.5	12.0	11.7	38.0
Caes. x Marq.	H-29-51	121.3	30.5	10.7	9.0	-
" x "	H-29-55	120.6	31.5	11.1	11.4	42.5
I-28-60 x Milt.	H-29-34	115.6	26.0	11.7	10.7	36.5
" x "	H-29-32	115.0	24.5	11.8	12.0	38.0
Milt. 0274	I-28-25	113.8	29.5	12.8	12.6	42.0
I-28-60 x Milt.	H-29-35	112.2	28.0	11.6	12.5	40.0

(continued)

TABLE XXIII (continued)

Variety	N.S.N.	Brooks			Edmonton	
		Yield in gms.	Ht. in inches	Protein %	No. of Tillers	Ht. in inches
Marq. x Caes.	H-29-48	111.5	28.5	11.9	9.2	40.0
Ceres	I-25-1	107.5	26.0	11.7	10.9	39.0
I-28-60 x Milt,	H-29-17	107.3	26.5	13.2	11.3	38.0
Reward x Caesium	H-29-23	106.4	28.5	12.1	12.5	-
Caes. x Marq.	H-29-73	106.2	27.0	11.1	10.8	40.0
" x "	H-29-71	106.1	28.5	9.9	11.5	40.0
Caesium .0111	I-28-20	105.7	29.5	11.0	12.3	41.5
I-28-60 x Milt.	H-29-43	104.5	24.5	12.7	11.1	42.0
Caes. x Marq.	H-29-50	103.8	29.5	11.0	9.6	41.0
I-28-60 x Milt.	H-29-41	102.8	25.5	12.8	12.0	38.0
" x "	H-29-9	101.5	25.0	12.3	9.1	42.0
" x "	H-29-31	100.4	25.0	13.0	12.9	42.0
" x "	H-29-7	100.1	26.5	12.0	12.5	37.5
Caes. x Marq.	H-29-69	99.3	29.5	11.6	9.6	41.0
I-28-60 x Milt.	H-29-12	98.7	27.0	11.6	11.5	37.0
" x "	H-29-4	98.3	29.5	12.1	10.7	41.0
Caes. x Marq.	H-29-61	98.3	31.5	10.7	13.8	41.0
I-28-60 x Milt.	H-29-5	97.2	24.0	13.4	11.3	-
Reliance	I-29-4	97.0	26.0	12.0	11.7	37.0
I-28-60 x Milt.	H-29-19	95.9	28.0	11.3	12.8	-
Caes. x Marq.	H-29-57	95.7	29.0	11.8	10.6	40.0
I-28-60 x Milt.	H-29-30	94.6	27.5	11.2	10.1	42.5
Reward x Caesium	H-29-24	94.5	28.0	12.2	10.5	35.5
Caes. x Marq.	H-29-52	93.7	26.5	12.1	11.7	42.0
Reward x Caesium	H-29-22	93.0	26.0	13.0	10.8	44.0
I-28-60 x Milt.	H-29-42	90.2	26.0	12.8	11.6	38.0
" x "	H-29-18	89.2	23.5	11.7	10.9	40.0
" x "	H-29-40	88.9	26.0	11.6	10.6	43.0
Caes. x Marq.	H-29-64	86.6	27.5	12.5	10.1	-
I-28-60 x Milt.	H-29-20	86.6	26.0	12.7	11.1	43.5
Caes. x Marq.	H-29-59	84.1	26.0	13.4	11.7	42.0
" x "	H-29-56	79.8	27.5	12.6	9.5	43.0
I-28-60 x Milt.	H-29-38	78.5	27.0	13.4	12.8	43.0
Caes. x Marq.	H-29-72	78.4	28.0	11.6	8.5	45.5
D. C.	I-28-60	77.6	27.5	12.0	10.2	3810
Reward x Caesium	H-29-27	75.1	25.0	12.2	12.0	40.0
Caesium x Marq.	H-29-70	74.0	24.0	13.1	7.9	41.5

(continued)

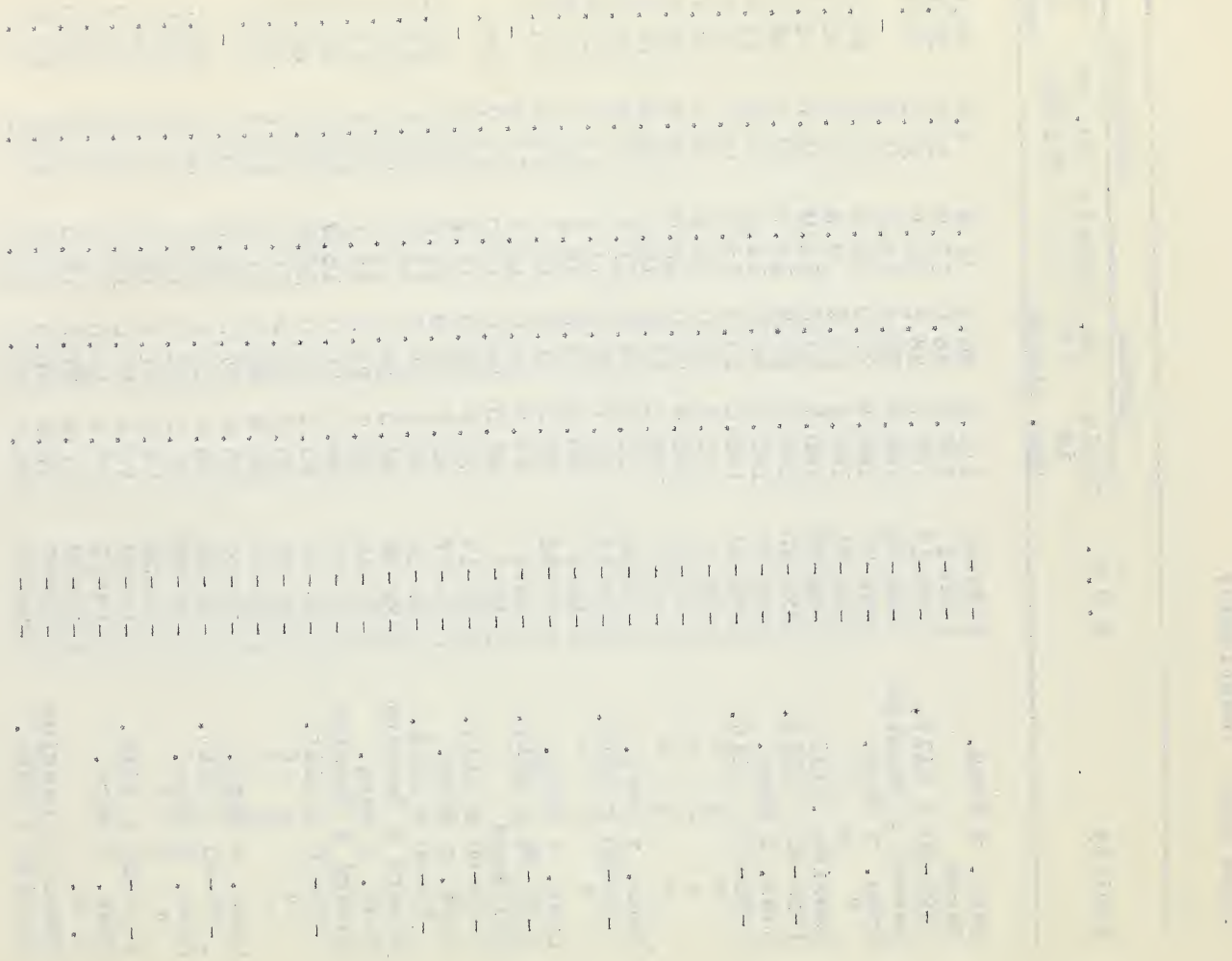


TABLE XXIII (continued)

Variety	N.S.N.	Brooks			Edmonton	
		Yield in gms.	Ht. in inches	Protein %	No. of Tillers	Ht. in inches
Hard Federation	I-28-35	73.9	21.5	12.2	13.7	38.0
I-28-60 x Milt.	H-29-29	73.8	28.0	10.2	12.4	41.0
Reward x Caes.	H-29-26	73.6	27.5	11.9	11.6	41.5
I-28-60 x Milt.	H-29-28	73.1	25.5	13.1	13.7	41.5
Mindum	I-36-100	72.2	30.0	11.5	9.7	42.5
Reward	I-25-21	71.2	28.5	13.2	8.3	39.0
I-28-60 x Milt.	H-29-10	68.2	21.5	13.7	8.9	40.0
Iumillo No. 7	I-36-104	67.4	22.5	11.9	11.1	37.5
I-28-60 x Milt.	H-29-39	65.6	25.0	14.1	9.7	36.5
" x "	H-29-21	64.4	26.0	13.3	11.4	-
Caes. x Marq.	H-29-60	63.0	25.0	12.4	11.6	-
Milturum .0321	I-28-14	60.0	25.0	12.9	15.5	41.0
Garnet	I-25-13	44.8	28.0	12.3	12.5	37.5
Reward x Caes.	H-29-25	40,8	24.0	14.8	9.0	36.5

In the tillering test at Edmonton the seventy-five varieties were planted in duplicate rows. The seed was spaced uniformly three inches apart in the row. The mean number of tillers varied according to variety from 7.9 to 17.9. In the analysis of the data by the variance method the significant difference of 4.1 corresponds approximately to the 5% point.

In order to test the significance of the yield data in Table XXIII an analysis was made using the variance method.

TABLE XXIV

Analysis of variance of the yield data obtained at Brooks, Alberta. (Data columns I to V inclusive)

	Degrees of Freedom	Sums of Squares	Mean Square	F.	5 %
Varieties	74	228,805.0	3,092.0	1.5	1.3
Replicates	4	65,082.6	16,270.7		
Columns	4	500,848.0	125,212.0		
Error	292	595,681.3	2,040.0		
Total	374	1,390,416.9			

S. E. of single plot = 45.2

S. E. of variety mean = 20.2

S. E. of difference of any two varieties = 28.6

Significant difference = 57.2

Significant differences were found between varieties. However, owing to the complete destruction by drought of part of column I* and considerable injury to column V, it seemed advisable to analyse the data in two additional ways, in one case omitting column I, and in the other column I and V. The analyses of these data are included in Tables XXV and XXVI.

TABLE XXV.

Analysis of variance of the yield data obtained at Brooks, Alberta. (Omitting the data of column I)

	Degrees of Freedom	Sums of Squares	Mean Square	F.	5 %
Varieties	74	227,742.4	3,077.6	1.4	1.5
Replicates	3	239,817.8	79,939.3		
Error	222	505,232.1	2,275.8		
Total	299	972,792.3			

S. E. of single plot = 47.7

S. E. of variety mean = 23.9

S. E. of difference of any two varieties = 33.8

* The test plot at Brooks was divided into 5 columns, according to the "Modified Balanced Block" method.

TABLE XXVI.

Analysis of variance of the yield data obtained at Brooks, Alberta. (Omitting the data of columns I and V)

	Degrees of Freedom	Sums of Squares	Mean Square	F.	5 %
Varieties	74	223,839.8	3,024.9	1.3	1.3
Replicates	2	52,458.8	26,229.4		
Error	148	349.548.9	2,361.8		
Total	224	625,847.5			

S. E. of single plot = 48.6

S. E. of variety mean = 28.1

S. E. of difference of any two varieties = 39.7

Significant difference = 79.4

In analysing the data when column I was omitted (Table XXV) the F value did not exceed the 5 % point, and when both columns I and V were omitted (Table XXVI) the F value was equal to the 5 % point. Therefore the greatest varietal significance was obtained when the complete data were used.(Column I to V inclusive.)

The lines were regrouped according to crosses and standard varieties. Table XXVII shows the mean yield and standard error of each cross and of the standard varieties grouped.

TABLE XXVII.

The mean yield of different crosses and standard varieties.

	No. of Lines	Mean Yield	Standard Error of Group Mean
F_7 Caesium x Marquis	21	103.8 gms.	± 4.41
F_7 I-28-60 x Milt. .0321	32	102.8 "	± 3.57
Standard varieties	16	97.3 "	± 5.05
F_7 Reward x Caesium	6	80.8 "	± 8.25

Lines of the cross Caesium x Marquis and I-28-60 x Milturum .0321 gave a higher yield than did the standard varieties, and these in turn outyielded lines of the cross Reward x Caesium.

VII. CHARACTER RELATIONSHIPS

As already indicated, one of the main purposes of this investigation is that of the identification of one or more characters associated with high yield under conditions of limited water supply.

The relationships between several characters were determined by means of the correlation coefficient. The results are summarized in Table XXVIII.

TABLE XXVIII.

Correlation coefficients between characters studied in the field and in the laboratory.

Variables correlated	No. of Varieties	Correlation Coefficient
Yield (Brooks) x Height (Edmonton)	66	+ .11
Yield (Brooks) x Height (Brooks)	75	+ .34*
Yield (Brooks) x Tillering (Edmonton)	75	+ .23**
Height (Brooks) x Height (Edmonton)	66	+ .55*
Height (Brooks) x Protein (Brooks)	75	- .67*
Yield (Brooks) x Protein (Brooks)	75	- .51*
Yield (Brooks) x (4 day) Sugar	17	+ .21
Morning period in Drought Machine x (4 day) Sugar	22	- .53**
Morning period in Drought Machine x Tillering (Edmonton)	18	+ .39

* Exceeds the 1 % point.
** Exceeds the 5 % point.

Considering the above correlations there are some indications that tillering capacity and height under Edmonton conditions are both associated with yield at Brooks. The tillering capacity of wheat plants may be important. Some plant breeders have selected on the basis of low tillering capacity. The reason for this is to be found in the fact that many tillers are arrested in their development, especially under dry conditions. Their production, therefore, is assumed to involve a loss to the general economy of the plant. It is reasonable to suppose, that branching above ground may be associated with extensive root development. If so, discarding lines characterized by extensive tillering may involve selection in the wrong direction. There is a highly significant correlation between the heights of varieties at Edmonton and Brooks. The level of significance falls well within the 5 % point. As expected, the height and yield at Brooks are correlated. The protein content of the varieties grown at Brooks is negatively correlated with height and yield.

The survival values obtained from the 4-day sugar run indicate a positive correlation with yield at Brooks and negative correlation with the morning period treatment made in the drought machine. This treatment on the other hand, shows a positive correlation with tillering at Edmonton.

DISCUSSION

It has been the aim of this investigation to develop methods useful in selecting wheat varieties for drought resistance and to identify as many characters as possible that are associated with yield under drought conditions. The methods of classification described in this paper are of little importance in themselves, but by considering them as a whole they may indicate one or more characters associated with yield under conditions of limited moisture supply. The error in the Brooks test in the summer of 1936 was so great that close relationships could not be expected. In spite of this some indications of success were evident. There was a significant relationship between tillering at Edmonton and yield at Brooks. Lines with twelve or more tillers per plants at Edmonton yielded fifteen percent more at Brooks than did lines with eleven tiller or less. Moreover, height of plant at Edmonton was weakly associated with yield at Brooks.

The drought machine and sugar tests have been considered largely from the standpoint of methods. However, certain interesting relationships were found from the data obtained. Highly significant differences were established between varieties in both these laboratory tests. High associations were

found between the three drought runs (6, 12 and 18-hour) in Experiment II and between the 6-hour runs of Experiment I and II. The 6-hour run indicated, from the results obtained, that this particular length of run is the most efficient for classifying varieties on the basis of response to artificial drought. The point has not been reached where it can be said that certain varieties are drought resistant and others non-drought resistant. However, some associations have been indicated between characters studied in the field with those studied in the laboratory. Tillering at Edmonton is weakly associated with the morning test in the drought machine, and this in turn is negatively correlated with the 4-day sugar treatment. The yield at Brooks,on the other hand, indicates a positive correlation with the 4-day sugar test.

It must be kept in mind that correlation coefficients should be considered only as indicative of certain relationships. These relationships even though only indicative, facilitate selection of the material subjected to field tests.

VIII. SUMMARY

The remodelling of the drought machine has led to a marked reduction in experimental error. Uniform wind conditions have been secured for all plants by means of an endless belt to which the pots are fastened. A return air flow has been constructed, which facilitates a temperature control within the range of one degree.

The results so far secured, all indicated that varietal differences with respect to treatment in the drought machine are highly significant. The relationships existing between the various runs (6, 12 and 18-hour), and between the 6-hour runs of different experiments have been discussed. The presence of a diurnal effect has been established; greater damage resulted from tests made in the drought machine during the morning hours from approximately 6 a.m. to 12 noon than during any other period of the day or night.

A method of testing the tolerance of young wheat seedlings to sugar solutions has been outlined with the hope that wheat varieties may be classified according to drought resistance by this means. The results so far indicate that varietal differences with regard to tolerance do exist. Higher significance with respect to varietal difference was obtained in the 4-day than in the 8-day

period. The relationships between the two laboratory methods and the field tests have been dealt with.

The possible utility of several characters has been investigated. The number of stomata per unit area has been determined in pentuplicate for 81 varieties. The mean values ranged from 114 to 226. Statistical analysis of the results reveal highly significant differences between the general means of varieties: a difference of 23 stomata corresponds approximately to the 5 per cent point. As the above measurements were taken in the field, a duplicate test was also made in the greenhouse last winter for the sake of comparison. The results from this test were unsatisfactory as growth of the plants was considerably retarded by the poor light conditions in January and February. The plants in general were small and etiolated.

Coefficients of correlation between various other characters, especially yield, height, tillering, protein content, are given and discussed.

ACKNOWLEDGMENTS

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